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Comparative analysis of the ecosystems in the northern Adriatic Sea and the Inland Sea of Japan: Can anthropogenic pressures disclose jellyfish outbreaks?

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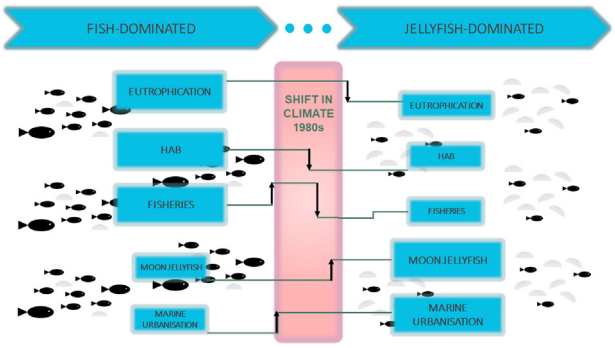
HIGHLIGHTS

- We reviewed environmental and ecosystem changes in two LTER sites in the N hemisphere.
- We examined the effects of anthropogenic pressures on moon jellyfish populations.
- A synchronous shift in climate was detected in the 1980s in both systems.
- Providing additional space for polyps, marine urbanisation-enhanced jellyfish population.
- Fish-dominated ecosystem switched to "jellyfish-permeated" environment.

GRAPHICAL ABSTRACT



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ABSTRACT

A prominent increase in the moon jellyfish (genus *Aurelia*) populations has been observed since 1980 in two semi-enclosed temperate seas: the northern Adriatic Sea and the Inland Sea of Japan. Therefore, we reviewed long-term environmental and biotic data from the two Long-Term Ecological Research (LTER) sites, along with the increase in the moon jellyfish occurrence to elucidate how these coastal seas shifted to the jellyfish-dominated ecosystems. The principal component analysis of atmospheric data revealed a simultaneous occurrence of similar climatic changes in the early 1980s; thereafter, air temperature increased steadily and precipitation decreased but became more extreme. Accordingly, the average seawater temperature from March to October, a period of polyps' asexual reproduction i.e. budding, increased, potentially leading to an increase in the reproductive rates of local polyp populations. Conspicuous eutrophication occurred due to the rise of anthropogenic activities in both areas from the 1960s onwards. This coincided with an increase of the stock size of forage fishes, such as anchovy and sardine, but not the population size of the jellyfish. However, by the end of the 1980s, when the eutrophication lessened due to the regulations of nutrients loads from the land, the productive fishing grounds of both systems turned into a state that may be described as 'jellyfish-permeated,' as manifested by a drastic decrease in fish landings and a prominent increase in the intensity and frequency of medusa blooms. A steady increase in artificial marine structures that provide substrate for newly settled polyps might further contribute to the enhancement of jellyfish population size. Elevated fishing pressure and/or predation by jellyfish on ichthyoplankton and zooplankton might jeopardize the recruitment of anchovy, so that the anchovy catch has

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never recovered fully. These semi-enclosed seas may represent many temperate coastal waters with increased anthropogenic stressors, which have degraded the ecosystem from fish-dominated to jellyfish-dominated.
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1. Introduction

Human impacts on marine ecosystems have accelerated dramatically in recent decades. These anthropogenic impacts, such as eutrophication, pollution, overfishing, land use change, and habitat loss, act additively and synergistically with climate change and severely impact the structure and dynamic of ecosystems worldwide (Halpern et al., 2015; Halpern et al., 2008). Recent climate studies have shown patterns of the world's oceans warming over the past 100 years (Burrows et al., 2011; Levitus et al., 2009; Parmesan and Yohe, 2003) and an increased variance of precipitation (Dore, 2005), that, more and more over the last 3–4 decades, have been affecting the physiology and phenology of organisms, species-specific spatio-temporal distributions, community taxonomic compositions, and food web dynamics (Parmesan and Yohe, 2003; Poloczanska et al., 2013; Jourdan et al., 2018). The removal of large apex consumers by fisheries has, in many marine ecosystems, caused trophic downgrading and a reduction of the food chain length (Estes et al., 2011), or led to regime shifts or alternative states of the ecosystem (Estes et al., 2011; Travis et al., 2014) where energy-poor species may dominate (Lynam et al., 2006). In addition, excessive coastline modification has led to habitat loss affecting species richness and abundances (Airoldi et al., 2008), while the proliferation of the artificial underwater structures may offer opportunities for some opportunistic species (Duarte et al., 2013).

The depletion of fish stocks, the modification of the natural coastline, eutrophication, and warming temperatures (Richardson et al., 2009) have created opportunities for the expansion of jellyfish populations worldwide (Brotz et al., 2012; Kawahara et al., 2006; Kogovšek et al., 2010; Purcell, 2012; Uye and Ueta, 2004). Several attributes of jellyfish biology, such as the short life-span of medusae, sexual and asexual reproduction, broad diets, passive feeding, and low metabolic requirements (Arai, 1997), enable them to not only reproduce rapidly when conditions are favourable, but also to tolerate some environmental stressors better than other organisms – one example being fish (Shoji et al., 2005). In such perturbed ecosystems, the role of jellyfish becomes more important, shifting energy from energy-rich fish to energy-poor jellyfish (Uye, 2011). Increased jellyfish populations may compete with fish for food (Purcell and Arai, 2001; Shoji et al., 2009) and prey on fish eggs (Gordoa et al., 2013; Zenitani et al., 2013) and fish larvae (Milisenda et al., 2014; Purcell et al., 2014; Sabatés et al., 2010). In addition, by clogging nets and stinging (De Donno et al., 2014; Nastav et al., 2013; Uye, 2008; Uye and Ueta, 2004), they severely affect fisheries (Conley and Sutherland, 2015; Palmieri et al., 2014) and the tourist industry (Ghermandi et al., 2015).

The cosmopolitan moon jellyfish of the genus *Aurelia* has been noted as conspicuous scyphozoan forming notorious blooms in a variety of coastal environments between 70°N and 40°S (Kramp, 1965; Russell, 1970). As the majority of the scyphozoan species, the moon jellyfish has a bipartite life cycle, alternating between the benthic polyp stage and the free-swimming medusa stage. Tiny polyps reproduce asexually to form clones and increase their numbers, while through strobilation, a single polyp produces and releases multiple planktonic ephyrae which grow into medusae. Adult medusae reproduce sexually to form planulae that attach onto hard substrates and develop into polyps. Each life stage can thrive in a wide environmental window of temperature, salinity, and/or food availability, yet, there are specific key environmental factors that determine the ontogenetic processes (Arai, 1997; Lucas et al., 2012). Experimental studies show that warmer temperatures favour budding (Han and Uye, 2010; Hubot et al., 2017; Malej et al., 2012), while a decrease in temperature leads to a specific threshold that triggers strobilation of moon jellyfish polyps originating from temperate zones (Han and Uye, 2010; Lucas et al., 2012; Purcell et al., 2012). Moreover, an abundant food supply stimulates polyp reproduction (Han and Uye, 2010; Hubot et al., 2017) and ephyrae production (Ishii et al., 2004). Such physio-ecological properties facilitate the proliferation of polyps that consequently leads to massive medusae outbreaks.

A recent study that analysed long-term changes in jellyfish abundance (Condon et al., 2013) failed to demonstrate robust evidence for recent jellyfish increase on a global scale and suggested that jellyfish populations oscillated with about a 20-year periodicity. However, there are many regional cases to demonstrate the increase in jellyfish populations (Boero, 2013; Brotz et al., 2012; Kogovšek et al., 2010). Among areas that experienced increased incidence of jellyfish blooms were the northern Adriatic Sea (NAD) and the Inland Sea of Japan (ISJ). Intensive jellyfish blooms were attributed to the medusae of the genus *Aurelia*, specifically to *Aurelia* sp. 8 in the NAD and *Aurelia* sp. 1 in the ISJ (Dawson, 2003), that were recently designated as *A. solida* and *A. coerula*, respectively (Scorrano et al., 2017). Despite the apparently different species, the main period of strobilation in both areas overlaps: it starts in late autumn, concomitant with seawater temperature decrease to or below 15 °C. In situ observations revealed, that in the NAD strobilation occurs between November and March (Malej et al., 2012), while in the ISJ the strobilation starts in December and lasts until April with ephyrae still persisting in net samples in May (Makabe et al., 2014). Medusae are generally present from February until June in the NAD with very rare observations in January and July (Malej et al., 2012). In contrast, longer seasonal occurrence of medusa from February until November characterises the coastal waters of the ISJ (Uye and Shimauchi, 2005).

Both systems are important fishing grounds and recent jellyfish outbreaks had significant impact on local fisheries by clogging fishing nets, reducing the quality of the fish catch, and increasing the cost of fishing operations due to their displacement and reparation of fishing nets (Nastav et al., 2013; Palmieri et al., 2014; Uye and Ueta, 2004). We therefore, exploited a long-term time series of environmental and biotic parameters from the two LTER (Long-Term Ecological Research) sites to detect and evaluate the environmental changes that promoted massive moon jellyfish outbreaks in the recent decades. It is believed, that two mechanisms are controlling how large-scale drivers affect the plankton community, and may result in favouring jellyfish: 1) increased nutrient loads and changes in nutrient ratios (i.e. eutrophication) often lead to an increase in biomasses at different trophic levels, shift the phytoplankton community from a diatom-dominated system to a flagellate-based food web (Mozetič et al., 2012), and result in the dominance of small-sized zooplankters (Conversi et al., 2009; Kamburska and Fonda-Umani, 2009), which all may benefit jellyfish blooms (Purcell, 2012) (i.e. bottom-up control); and 2) overharvesting of forage fish relinquishes the competition for food between forage fish and jellyfish, leading to environmental conditions in which jellyfish flourish (Purcell, 2012) (i.e. top-down control). To investigate that, long-term changes in climate, nutrient loadings, and total fish catch were analysed. Finally, we hypothesised that the increasing seawater temperature together with marine urbanisation stimulated polyps' population in the way that resulted in an increase in frequency and intensity of medusae blooms.

2. Materials and methods

2.1. Study areas

The NAD and the ISJ, are semi-enclosed temperate seas in the northern hemisphere (Fig. 1), having comparable surface area, average depths, volumes, river inflows, annual seawater temperature ranges, and human populations in the coastal zones (Table 1). The NAD (12°12′–13°48′E and 44°00′–45°47′N) is the shallowest and the northern-most area of the Adriatic and Mediterranean Seas with an average depth of 34 m and an area of 19,000 km^2 holding 635 km^3 of seawater. About 10,000 km westward from the NAD, lies the ISJ (130°40′–135°30′ E and 32°55′–34°50′N). Locked between the islands of Kyushu, Shikoku, and Honshu, it extends about 450 km from east to west and 15–55 km north to south, with an area of 23,203 km^2, a seawater volume of 882 km^3, and an average depth of 38 m. The NAD receives 90,000 km^3 of river discharge annually, a higher river inflow than what flows into the ISJ (50,000 km^3) due to its wider watershed. The coastal areas of both basins are highly populated with a population inhabiting the coastal regions of the NAD and the ISJ of 25 and 30 million, respectively.

2.2. Data

Monthly means of air temperature (°C) and relative humidity (%) at 1000 hPa pressure, sea surface temperature (°C), sea level pressure (mb), precipitation rate (mm day^{-1}), and top of the atmosphere outgoing longwave radiation (OLR) (W m^{-2}) data were provided by the NCEP Reanalysis performed by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (accessible at http://www.esrl.noaa.gov/psd/). The temporal coverage of the time series data was as available, from January 1948 to December 2016, representing the geographic areas between 42.5°N–46.7°N and 11.3°E–15.0°E for the NAD, and 130.0°N–135.0°N and 31.4°E–35.0°E for the ISJ. Principal component analysis (PCA) was performed on the standardised time series of monthly means for each basin (normalised by z-score transformation $z = x - \mu / \sigma$, where μ is the mean and σ is standard deviation), and the first two components (PC1 and PC2) were further used as a climate proxy to describe the climate variability in each basin. To detect if and when significant changes in climate occurred, PCA was performed on yearly means, and change point analysis was then performed on PC1 and PC2 (Change-Point Analyzer 2.3 software; Taylor Enterprises, Libertyville, Ill). After that, the Mann-Kendall test and the non-parametric Sen's method (MAKESENS template in the Microsoft Excel) were used to quantify the magnitude of the trend within the period between the points of significant changes detected in the previous step (Salmi, 2002).

Table 1
Comparison of basic dimensions and other properties between the northern Adriatic Sea and the Inland Sea of Japan.

	northern Adriatic Sea	Inland Sea of Japan
Area (km^2)	19,000	23,203
Average depth (m)	34	38
Seawater volume (km^3)	635	882
River discharge (km^3 y^{-1})	90,000	50,000
Rain catchment area (km^2)	118,000	47,895
Annual temperature range (°C)	9–25	10–28
Population (millions)	25	30

Detailed analysis of sea temperature variability was performed on *in-situ* daily measurements. In the NAD, the temperature was measured daily at 2 m depth in an outer quay of the harbour of Trieste (45°38′59″ N, 13°45′08″ E) from January 1934 to December 2016. Data are archived at CNR, the Institute for Marine Sciences in Trieste. In the ISJ, the sea surface temperature was measured daily at Hiroshima Prefectural Marine Technology Centre (34°10′20″ N, 132°33′22″ E) from 1970 up to the present. The data file was kindly provided from the Centre.

The data of total riverine nutrient loading into the NAD, that also incorporate the sewage discharges, were gathered from the publications (Cozzi and Giani, 2011 and the references therein). For the ISJ, such data were obtained from a previous publication (Li et al., 1995) as well as by the Ministry of Environment data available from Setouchi Net (https://www.env.go.jp/water/heisa/heisa_net/setouchiNet/seto/index.html).

Annual occurrences of red-tides or harmful algal blooms (HAB) in the NAD were derived from previous publications (Fonda Umani et al., 2004; Fonda Umani et al., 1992; Marić et al., 2012; Mikaelyan et al., 2014), while the data for the ISJ are available on Setuchi Net (see above).

The number of offshore platforms installed in Italian and Croatian waters (years of construction are available from EEA (https://www.eea.europa.eu/data-and-maps/figures/locations-of-major-offshore-installations-1) and CHA, 2015) were used as a proxy of marine urbanisation or coastline modifications in the NAD. The dataset of annual reclamation land areas between 1965 and 2012, and intermittent (1979, 1984, 1993 and 1996) reports on the type of seashore coverage, both being available from Setouchi Net, were used in the ISJ.

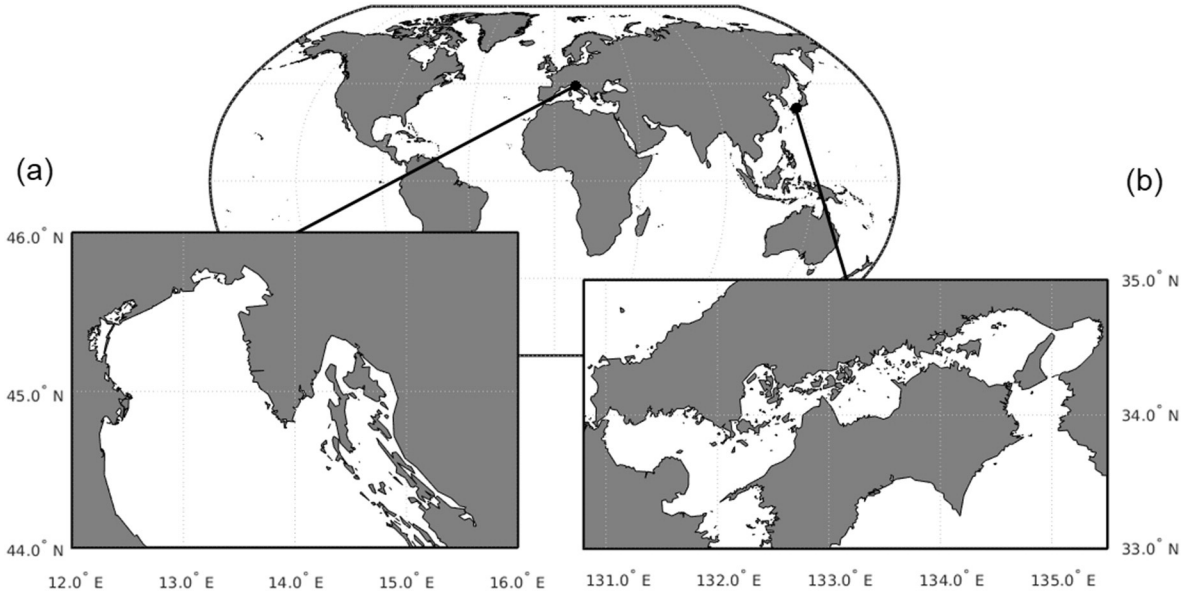

Fig. 1. Study areas: the northern Adriatic Sea (12°12′–13°48′ E and 44°00′–45°47′ N) (a) and the Inland Sea of Japan (130°40′–135°30′ E and 32°55′–34°50′ N) (b).

The dataset of yearly occurrence of the moon jellyfish in the NAD, previously published in Kogovšek et al. (2010), was updated to include the data until 2016. The observations were then pooled per decade and expressed as the number of years with medusa occurrence per decade. Temporal changes in relative abundances of moon jellyfish in the ISJ were estimated based on the results of two polls of fishermen conducted in 2002 (Uye and Ueta, 2004) and 2012 (Uye, unpublished). In the first survey, a total of 1152 fishermen with >20-year experience replied in which 5-year periods in the last 20 years (i.e. 1983–1987, 1988–1992, 1993–1997, and 1998–2002) they had observed the most prominent increase of moon jellyfish. In the second survey, a total of 50 fishermen answered about the relative abundance of medusae in the recent decade (2003–2007 and 2008–2012) compared to the abundance in the preceding 5-year period (i.e. 1997–2002).

In addition, a semi-quantitative monthly time series from January 1983 to December 2014 has been constructed from field observations and evaluated data obtained from citizen science in the NAD. A value between 0 and 3 was attributed to each month according to the following criteria: when medusa were not observed, a 0 value was attributed to that month; a value of 1 corresponds to the situation on the field when sporadic events of individual organisms was noted; 2 was attributed when individual medusae were frequently observed and/or, when medusae were forming larger aggregations; and 3 represents the months when larger aggregations were frequently observed, as well as blooming events.

The annual fish landings dataset for the northern and central Adriatic Sea in the years between 1970 and 2014 was retrieved from the FAO database (Fishstat+, FAO, 2016). The fishing area (Division 37.2.1) is defined as the waters of the Adriatic Sea north of a line running from the Albanian northern frontier on the east coast of the Adriatic Sea due west to Cape Gargano at 41°49′N latitude and 16°12′ E longitude on the coast of Italy. The annual fish catch statistics for the ISJ have been archived by the Seto Inland Sea Fisheries Management Office and the data for the period between 1952 and 2015 are available on their website: http://www.jfa.maff.go.jp/setouti/tokei/seisansuii.html.

3. Results

3.1. Environmental and anthropogenic drivers

3.1.1. Climate change

The first two components (PC1 and PC2) of the PCA were used as a proxy to describe changes in climate, as together they described the majority of the variation in the data (67% and 82% of the total variance for the ISJ and the NAD, respectively) (Table 2). In both areas, the first principal component (PC1) correlated with relative humidity (0.58 and 0.48 in ISJ and NAD, respectively) and precipitation ($r = 0.57$ and 0.49 in ISJ and NAD, respectively), and correlated negatively with the top of the atmosphere outgoing longwave radiation (ORL) ($r = -0.55$ and -0.53 in ISJ and NAD, respectively) (Table 2). In addition, in the NAD the PC1 also correlated with pressure at sea level ($r = -0.42$). The second principal component (PC2) was in both areas in majority describing the variability in sea and air temperature ($r = 0.70$ for both in the ISJ and $r = 0.66$ and 0.69 in the NAD for air and sea surface temperature, respectively).

The point change analysis performed on PC1 and PC2 of yearly means revealed an almost synchronous significant change in PC1 for both systems, in 1982 in the ISJ and in 1981 in the NAD. In addition, significant changes in 1956 in $PC1_{ISJ}$ and 1970 in $PC1_{NAD}$ were also detected. A significant decreasing trend in $PC1_{NAD}$ and $PC1_{ISJ}$ was determined until the early 1980s (slope: -0.053, $\alpha = 0.1$ and slope: -0.058, $\alpha = 0.01$ for $PC1_{ISJ}$ and $PC1_{NAD}$, respectively), and which reversed after 1982, but only in $PC1_{ISJ}$ ($\alpha = 0.01$). These changes were very sudden and occurred uniformly throughout the year, and can also be detected in the PCA analysis performed on monthly means (Fig. 2). After the 1981/1982, negative PC1 anomalies were characteristic throughout the year, especially until the late 1990s for the $PC1_{ISJ}$; after that, positive anomalies were characteristic during autumn. These results indicate a change toward a climate characterised by a decline in the amount and higher annual variability of precipitations that occurred mostly in winter, summer, and autumn over the NAD, and in autumn over the ISJ.

Table 2
PCA coefficients and the total variance described by each of the first three principal components (PC). Significant correlations are marked in bold (confidence level $\alpha = 0.05$).

tot variance	The Inland Sea of Japan			The northern Adriatic Sea		
	36%	31%	17%	51%	31%	9%
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
Air T	−0.03	**0.70**	0.01	−0.22	**0.66**	−0.11
SST	−0.04	**0.70**	0.06	−0.15	**0.69**	0.12
ORL	**−0.55**	0.05	−0.28	**−0.53**	−0.03	−0.17
Rel hum	**0.58**	0.06	0.19	**0.48**	0.21	0.44
Precipitation	**0.57**	0.06	−0.13	**0.49**	0.15	0.11
Sea Level Pressure	−0.20	−0.04	**0.93**	**−0.42**	−0.14	**0.86**

Significant changes in $PC2_{ISJ}$ of yearly means were detected in 1980, 1988, and in 1998, while in $PC2_{NAD}$ significant shifts were determined for 1962 and 2011. In the ISJ, a trend toward negative anomalies was detected until 1988, followed by a stepwise increase toward positive anomalies, especially after 1998. Similar changes, yet not significant in the NAD, that occurred almost synchronously in both basins, were also detected in the PC2 of monthly means (Fig. 2); a period of negative anomalies, indicating lower temperatures than long-term monthly averages were detected between the beginning of the 1970s and late 1980s, followed by a period of positive monthly anomalies, mostly from late spring to early autumn.

3.1.2. Seawater temperature

A closer inspection of yearly anomalies calculated from the daily in situ measurements of the sea temperature confirmed the trend detected in the PC2s (Fig. 3). After a decade of colder years than-long term average between the 1970 and mid-1980s, the average yearly sea water temperature started to increase in both basins from 1981 and 1982 onward, and from the turn of the millennium. Moreover, a majority of years were up to 1 °C warmer than the long-term average. The yearly average seawater temperature increased as a result of warmer autumns and winters, while the spring and summer anomalies were more variable over the last three decades.

The moon jellyfish polyps asexually reproduce by budding from spring to autumn, i.e. from March to October (Makabe et al., 2015; Malej et al., 2012). In the NAD, the seawater temperature during the period of asexual reproduction was on average 18.3 °C (Fig. 4a) until 1980. After the shift in climate in the 1980s, the seawater temperature was steadily increasing by 0.26 °C per decade, reaching values above 19.0 °C after the year 2000. A similar trend was observed in the ISJ; the average seawater temperature for the period between March and October was steadily increasing over the investigated period (dataset available from 1970 on) with the rate of 0.21 °C per decade (Fig. 4b), yet with higher long-term average value of 19.5 °C (for the period 1981–2016) than in the NAD (18.6 °C).

3.1.3. Eutrophication

Higher nutrient loads, in particular phosphorous, were characteristic in the 1960s, 1970s, and 1980s for both areas, followed by a decreasing trend in total N (TN) and total phosphorous (TP) in the ISJ and a reduction of TP in the NAD. No clear trend in TN loadings into the sea was observed in the NAD. The TN loadings into the NAD fluctuated within the range of 244 and 339 ton N day^{-1} over the years – with a marked exception in 2004 when up to 632 ton N day^{-1} was introduced into the sea (Table 3). In contrast, TP loads fluctuated between 32 and 43 ton P day^{-1} in the 1970s and 1980s, after that, a decreasing trend

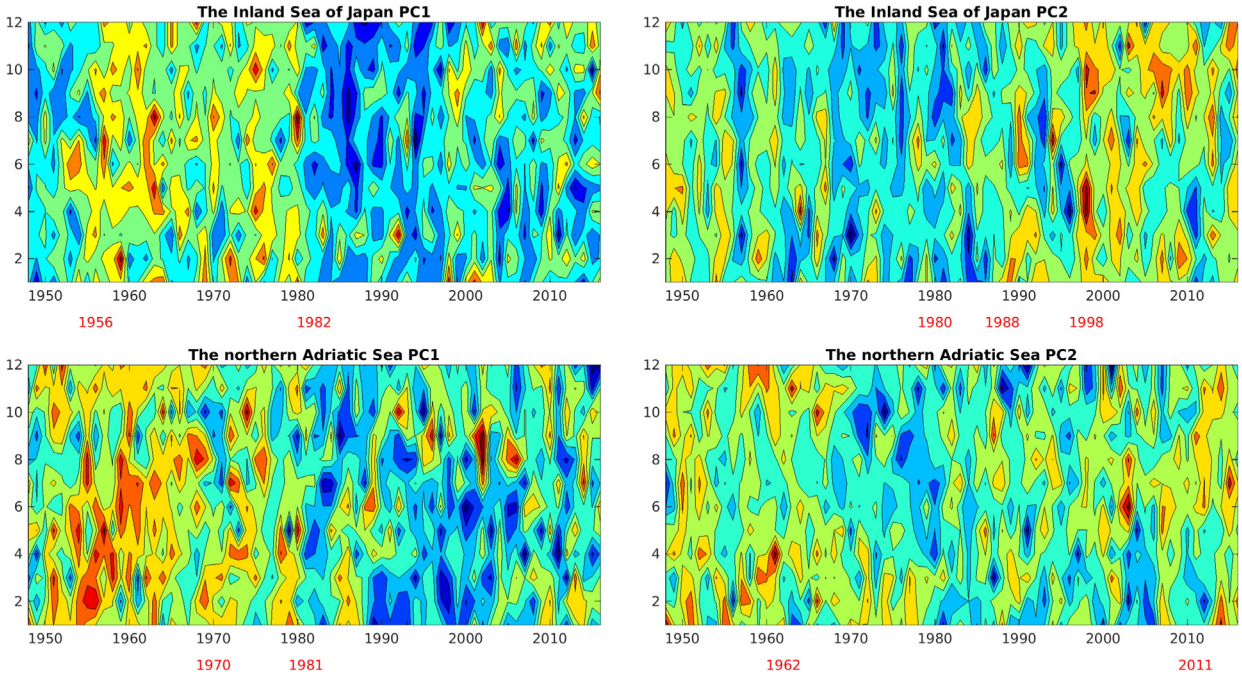

Fig. 2. Principal components (PC1 and PC2) of monthly means. The years with significant shifts that were detected in principal components of yearly means are marked red.

was detected in the riverine TP discharging into the sea, from 22 ton P day^{-1} in the late 1990s to only 12 ton P day^{-1} in 2007. The daily amount of TN and TP discharges into the ISJ (Fig. 5) were higher compared to the ones detected in the NAD. In the ISJ, TP loads sharply decreased from maximum 66 ton P day^{-1} in 1979 to ca. 49 ton P day^{-1} in 1984, thereafter TP loads gradually declined until reaching 28 ton P day^{-1} in 2009. A marked decrease was also recorded in TN loadings, from an average 707 ton N day^{-1} between 1979 and 1994, to 596 ton N day^{-1} in 1999. This progressively decreased thereafter, reaching 433 ton N day^{-1} in 2009.

Due to a sharp decreasing trend in TP, but fluctuating TN loadings in recent decades in the NAD, the molar N:P ratio progressively increased. The molar N/P ratio fluctuated between 14.1 and 18.7 in the years between the 1970s and early 1990s, after that it increased to 33.4 in the late 1990s and to 56 in 2007. Conversely, in the ISJ the molar ratio fluctuated between 30 and 40, indicating a synchronous decrease in both, TP and TN into the basin.

The progression of the eutrophication has caused an exponential increase in the number of the HAB events. In the NAD, the HAB events were more frequent in the decade between 1977 and 1986, with such events recorded every year (Fig. 6). After that, there were no such events recorded in the NAD until 1997, when only nine years were characterised by HAB events until 2012. In the ISJ, the total incident of the HAB in 1967 was 48, remarkably increased thereafter and reached its maximum of 299 in 1976 (Fig. 6). After this peak value, the number of yearly occurrences has shown a decreasing trend to around 100 per year, and has fluctuated around that value ever since, following the decreasing trend of nutrient loads into the ISJ.

3.1.4. Marine urbanisation

The moon jellyfish polyps were reported to be attached onto natural secondary substrate (predominantly on oysters) on offshore platforms, as well as in the majority of the commercial ports in the Adriatic Sea (Vodopivec et al., 2017). Therefore, the number of installed offshore platforms were used as a proxy for historical marine urbanisation. The first offshore platform was installed in 1968 (Fig. 7) and by the end of the decade, five additional platforms became fully operational. In the following decades the number of installed offshore constructions increased exponentially, with the highest number of installed platforms per decade (41) in the 1980s, and reached 137 by 2011. Such a rapid increase of the artificial structures in the last four decades in the NAD coincided with the sharp increase in the number of years with medusa occurrence per decade detected in the 1980s (see detailed description below) (Fig. 9a).

The coast of the ISJ was exposed to drastic and extensive modifications in the last half century. In the 1960s and 70s, nearly 20,000 ha of shallow seas was reclaimed mainly for the land of new factory constructions associated with Japan's economic development (Fig. 8). After 1980, the reclamation steadily continued, but at a much slower pace than before. The area of artificial coastal surface covered with concrete progressively increased due to losing pristine natural coastline. The percentage of artificial surface increased from 44% in 1978 to 49% in 1996 (Fig. 8).

3.2. Variation in jellyfish occurrence and jellyfish-fish interaction

3.2.1. Seasonal and inter-annual dynamics of moon jellyfish

The long-term time series of moon jellyfish observations in the NAD revealed a sharp increase in the number of years with medusae occurrence per decade in the 1980s (Fig. 9a). Eight out of ten years, medusae were observed in the 1980s and 1990s, while from 2000 onward (2000 to 2010) medusae were observed every year. The seasonal occurrence of the moon jellyfish spanned between March and June (Fig. 10), with some years young medusae being observed as early as January (in 2010, 2011 and 2013; an exception was 2009 in which a young medusa was observed in December) and were present until July (in 1989 and 2011). The extensive occurrence (i.e. blooms) were detected mostly between March and May, with the exception of 2011 when blooms were observed in February, as well as in 1989, 2004, and 2008 in which the massive occurrence lasted until June. From 2004 onward, the season of moon jellyfish occurrence became longer, as the medusae appeared earlier and disappeared from the water column later in the season. In addition, the blooms became more extensive with lesser inter-annual variation.

In the first poll survey conducted in 2002, with a total of 1152 respondents, 65% replied that medusae in the ISJ had increased in the

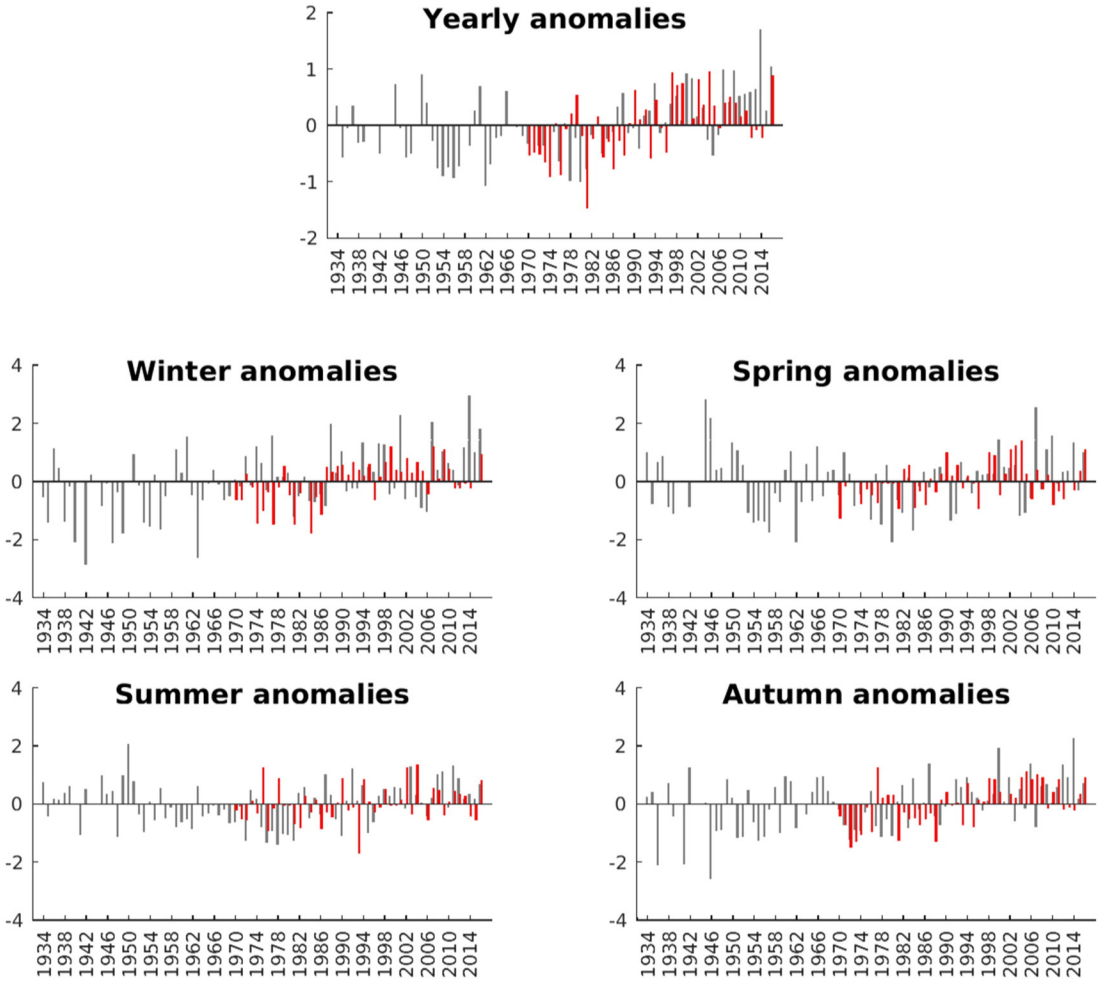

Fig. 3. Long-term yearly and seasonal sea surface temperature anomalies of daily in situ measurements in the northern Adriatic Sea (grey) and the Inland Sea of Japan (red). Average value for January–March was attributed to winter, April–June to spring, July–September to summer and October–December to autumn.

last 20 years (1983–2002) compared to the population level prior to 1983. Further, they pointed out the different periods when moon jellyfish had shown the most prominent increase: 11% for 1983–1987, 17% for 1988–1992, 41% for 1993–1997, and 32% for 1998–2002 (Uye and Ueta, 2004). An assumption was made rather intuitively that these frequencies might roughly represent the relative abundance of the moon jellyfish for the latest 20 years, being ranked as 1.0 for 1983–1987, 1.5 for 1988–1992, 3.7 for 1993–1997, and 2.9 for 1998–2002 (Fig. 9b). In the second survey (Uye, unpublished), respondents from a total of 50 fishermen split evenly: 50% of them answered they had observed a decrease, and the remaining 50% reported no change in medusa abundance during the recent 10 years (2003 − 2012) compared to the preceding five years (1998–2002). Of those who observed a decrease, 40% replied it had occurred in years between 2003 and 2007, and 60% in 2008–2012. Hence, we assumed that the relative abundance of moon jellyfish to be 2.9 for 2003–2007, the same level as for 1998–2002, and it decreased to 2.0 for 2008–2012 (Fig. 9b). These poll results indicate that medusa population in the ISJ increased gradually from the 1980s, remarkably in the 1990s to attain a peak in the mid 1990s, and thereafter declined.

3.2.2. Fish catch and jellyfish – fish interaction

The total annual fish landings in the Adriatic Sea sharply increased from 107×10^3 ton in 1970 to a peak of 183×10^3 ton in 1981 (Fig. 11a). During 7 years, between 1979 and 1983, it remained at high levels (annual average: 228×10^3 ton), followed by a rapid decline to 89×10^3 ton in 1991. The catch was kept relatively low until a gradual increase started in 2005, reaching 130×10^3 ton in 2014. In the ISJ (Fig. 11b), the total annual fish catch gradually increased from 181×10^3 ton in 1952 to 436×10^3 ton in 1972, remaining at a high level until 1986 (a maximum of 462×10^3 ton was recorded in 1982). Then, it steadily declined to 154×10^3 ton in 2015. Interestingly, the periods of peak landing in both systems overlapped: from 1978 to 1983 in the Adriatic Sea, and from 1972 to 1986 in the ISJ.

The small pelagic fishes, anchovies and sardines, are very important target species for fisheries in both systems, accounting on average for 44% and 38% of total fish catch in the Adriatic Sea and the ISJ, respectively (averaged landings for the periods 1952–2015 and 1970–2014 for the ISJ and the NAD, respectively) (Fig. 11). The years of maximum catch coincided in both systems: 1981 in the Adriatic Sea (123×10^3 ton) and 1982 in the ISJ (244×10^3 ton). The ratio of small pelagic fishes of the total fish catch gradually increased in the Adriatic Sea, mostly from the end of the 1980s onward, while it remained relatively constant in the ISJ. In the period between 1985 and 1993, anchovy fisheries in the Adriatic Sea almost collapsed. The total annual catch of anchovy dropped from 41×10^3 ton in 1985 to barely existent 7×10^3 ton in 1993.

In the Adriatic Sea, anchovy spawns in the shallow coastal areas along the Italian coast of the northern and central Adriatic Sea, in particular off the Po River mouth (Morello and Arneri, 2009) from April to October (Regner, 1996). The spawning season coincides spatially and

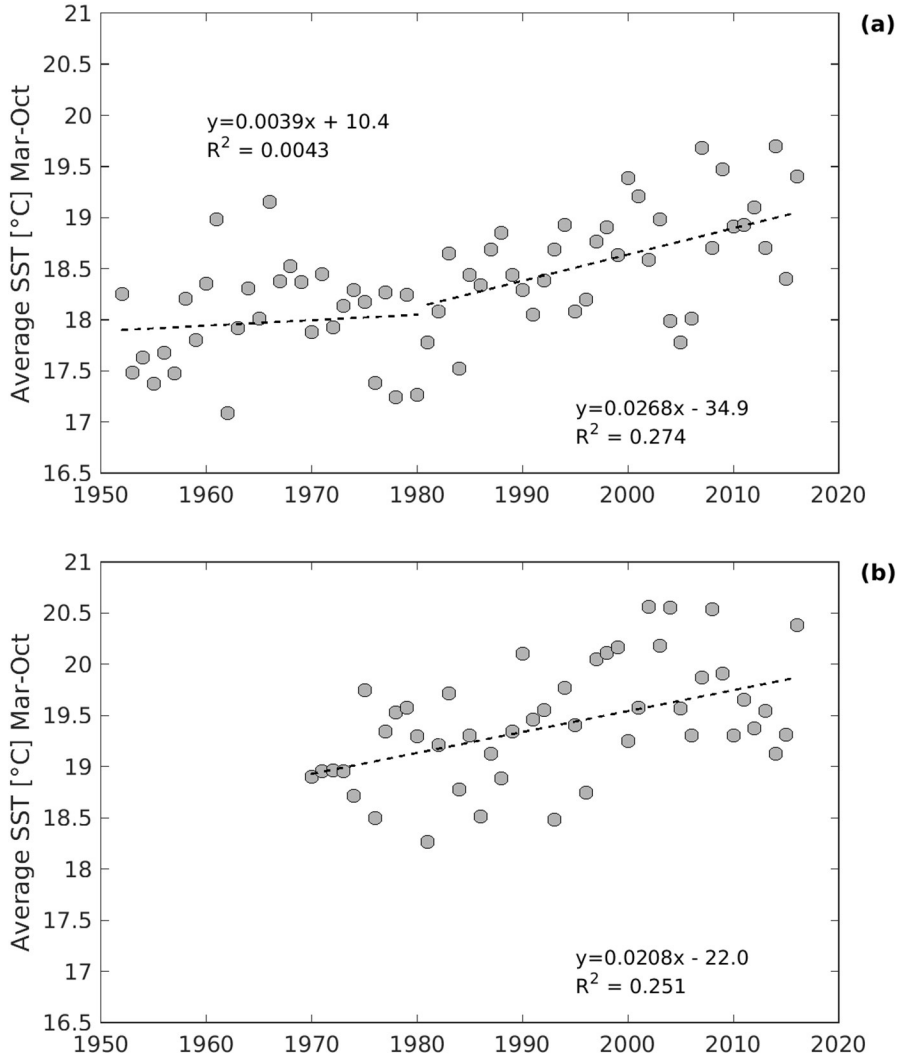

Fig. 4. Average seawater temperature during the period of polyp asexual reproduction (budding) (from March to October) in the northern Adriatic Sea (a) and the Inland Sea of Japan (b).

partly temporarily with the occurrence of moon jellyfish (Fig. 10) in the same areas. Recurrent and extensive occurrence of jellyfish during spawning season of anchovy may drastically affect the fecundity of fish by competing for food and successful recruitment of this planktivorous fish through predation on ichthyoplankton and consequently, the spawning biomass of the following year. Therefore, we investigated the correlation of the spawning biomass of anchovies with the frequency of medusa occurrence during anchovy spawning season (Fig. 12). An opposite trend was observed between the two parameters. During the years with 3 to 5 months of medusa occurrence per year (1987–1989 and 1998) the anchovy spawning biomass was low. Indeed, a negative correlation ($r = -0.29$, Spearman's rank correlation coefficient) was detected between the number of months with medusa

Table 3
Nutrient loadings (TN-total nitrogen and TP-total phosphorus) into the northern Adriatic Sea (after Cozzi and Giani, 2011).

	TN load (ton day^{-1})	TP load (ton day^{-1})	N to P ratio
1974–1978	243.84	32.33	16.6
1976–1978	312.33	42.74	16.1
1979–1984	301.37	40.27	16.4
1982–1987	473.97	35.34	29.5
1996–2000	473.97	22.19	46.9
2004	634.54	28.95	48.2
2005	339.07	15.91	46.8
2006	322.12	13.82	51.2
2007	300.32	11.74	56.2

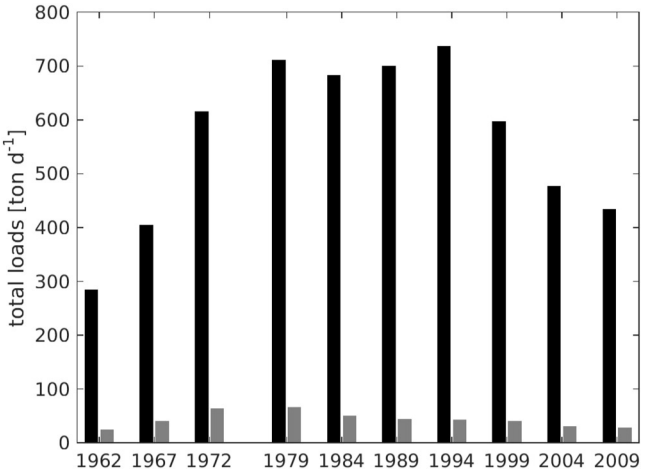

Fig. 5. Total nutrient loads into the Inland Sea of Japan; TN-total nitrogen (black) and TP-total phosphorous (grey).

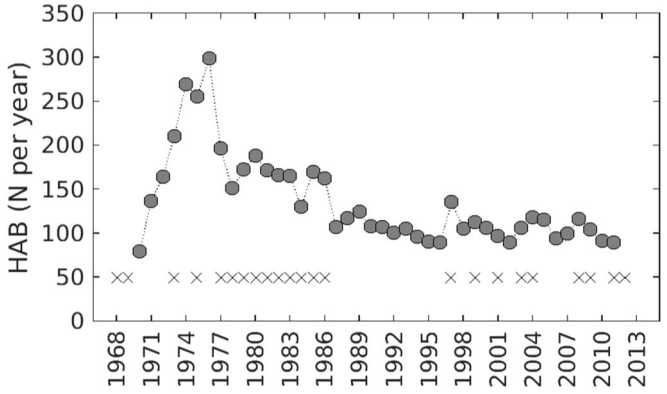

Fig. 6. The number of harmful algal blooms occurrence per year in the Inland Sea of Japan (filled circles). The years with HAB recorded in the northern Adriatic Sea are marked with cross. The later dataset was compiled from Fonda Umani et al., 1992, Fonda Umani et al., 2004 and Mikaelyan et al., 2014.

occurrence during anchovy's spawning season, and the biomass of spawning anchovy (data from Cingolani et al., 2003 for the period between 1983 and 2002). This correlation increased one-year lag ($r = -0.47$) and two-year lag ($r = -0.48$), confirming the negative impact of medusae on anchovy stock size.

4. Discussion

A synchronous change in climate was detected in the early 80s in both areas, interpreted as changes in precipitation pattern and increase in air and seawater temperature. Our results were in accordance with the previously detected decreasing trend in total rainfall over Japan (Xu et al., 2002) and over the Mediterranean Sea (Alpert et al., 2002) with an average reduction of about 10–20% (Romero et al., 1998). In spite of the decline in total rainfall, extreme daily rainfall has been increasing in recent decades over both basins (Alpert et al., 2002; Xu et al., 2002; Zanchettin et al., 2008). Such increase in the variance in the rainfall distribution was linked to global warming due to the increased water vapour and warmer air (Dore, 2005). Consequently, substantial spatial and temporal changes in rainfall pattern significantly alter the watersheds. Indeed, the runoff of the major river discharging into the NAD has been decreasing since the 1940s (Zanchettin et al., 2008), and the flow rate of the minor rivers was also reduced by 33% since 1980 (Cozzi and Giani, 2011). Concomitant decrease in nutrient discharges was observed with a reduced river runoff (Cozzi et al., 2012; Cozzi and Giani, 2011), turning the trend toward more oligotrophic waters (Mozetič et al., 2010).

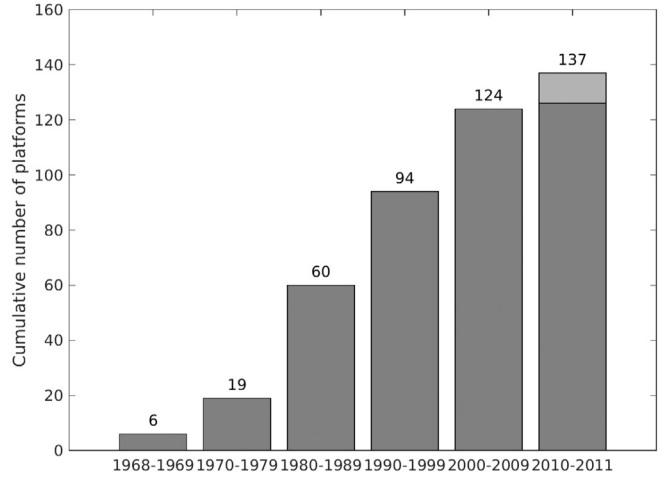

Fig. 7. Cumulative number of offshore platforms in the northern Adriatic Sea (light grey colour marks the 10 platforms for which the information about the date of installation was not available).

Before the above described climatic change occurred, both systems faced serious eutrophication from the 60s onward, due to the increase of human activities upon the coastal areas, that gave rise to recurring HAB events causing serious economic loss in fisheries, poisoning cultured fish and bivalves. The major nuisance algal taxa in the NAD were dinoflagellate, like *Peridinium*, *Gymnodinium*, *Gonyaulax*, *Glenodinium* (Fonda Umani et al., 1992) while only *Noctiluca scintilas* bloom incidence were recorded after 1986 onward (Fonda Umani et al., 2004; Mikaelyan et al., 2014). On the other hand, in the ISJ, diatoms dominated in the late 1970s and early 1980s, and raphidophytes (i.e. *Chattonella* spp.) were significant in the mid-1980s, and dinoflagellates (*Karenia mikimotoi*, *Hetercapsa circularisquama*, *Gonyaulax polygramma* and *Cochlodinium polykrikoides*) prevailed among the red-tide forming taxa in the 1990s (Imai et al., 2006; Yamamoto, 2003).

To stop the increasing eutrophication, laws regulating the discharge of nutrients were put in place. In 1973, regulation of organic substances in terms of chemical oxygen demand was established in the ISJ and more constraining controls of TP and TN loads were further implemented in 1979 and 1996, respectively. In the NAD, only TP discharge was regulated and it was implemented by a legislative act banning the use of phosphates in the detergents in the mid-1980s. Concomitantly, the general improvement in sewage treatment further reduced nutrient inputs in the NAD and its watershed. As a consequence of such measures, the TP and TN loads into the basins gradually decreased, yet at different rates indicated by difference in N to P ratio from the 1980s onward in both basins (Fig. 5, Table 3). Consequently, HAB incidence, that dominated the period until late 1980s dwindled in the ISJ, likewise only few HAB events were observed in the NAD ever since (Fig. 6).

The period between 1960 and 1990 was not only characterised by increasing eutrophication, but also by high biomass of forage fishes. High total annual catch in planktivorous fish was reported in the late 1970s and 1980s with the maximum annual catch, dominated by anchovies, recorded in the early 1980s. After a few consecutive years of record anchovy catches, the anchovy fishery almost collapsed in both basins. In the ISJ, it decreased to less than one third by 1996 (Nagai, 2003), while the historical minimum was reached in 1987 in the NAD, and it started to recover only after 1996 (Morello and Arneri, 2009). Low levels of anchovy recruitment coincided with a drastic increase of medusa population outbreaks from the 1980s and 1990s onward in both study areas. Also, an inverse relationship between the duration of medusa occurrence and the timing of anchovy spawning was detected (Fig. 12). Similarly, a negative relationship between jellyfish and forage fish has previously been observed in the North Sea, the Eastern Bering Sea, as well as northern California Current system and the Humboldt Current system (Brodeur et al., 2014; Lynam et al., 2005; Mianzan et al., 2014; Ruzicka et al., 2012). In the NAD and in the ISJ, the spatial and temporal distribution of the moon jellyfish and anchovy overlaps (Morello and Arneri, 2009; Regner, 1996; Shoji et al., 2009, this study), increasing the potential for resource competition and predation as jellyfish diets often include fish eggs and fish larvae (Gordoa et al., 2013; Purcell and Arai, 2001; Purcell et al., 2014; Robinson et al., 2014; Shoji et al., 2005; Shoji et al., 2009). Thus, elevated fishing pressure and predation by medusae on ichthyoplankton and zooplankton would thus have negatively affected recruitment of anchovy larvae, as well as recovery of the anchovy fishery, after the collapse at the end of the 1980s and beginning of the 1990s.

The rise in the moon jellyfish population outbreaks from the 1980s and 1990s onward, was concomitant with two major environmental changes: 1) a continuous increase in the average seawater temperature from March to October, during which asexual reproduction of polyp populations in both regions takes place, and the absence of extreme low winter temperature events; and 2) the proliferation of artificial underwater structures constructed during recent marine urbanisation,

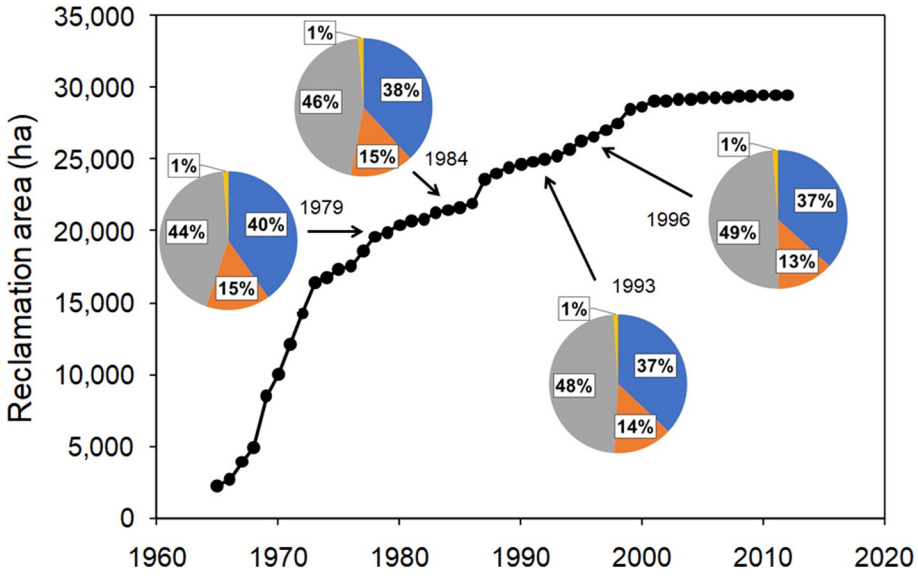

Fig. 8. Cumulative area of reclamation along the coast of the Inland Sea of Japan (black line) and the type of the seashore coverage (%); yellow – estuary; blue – natural seashore; orange – seminatural seashore; and grey – artificial seashore.

providing new habitats for polyps. The average seawater temperature has been increasing at rates of 0.27 and 0.21 °C per decade since 1980 in the NAD and the ISJ, respectively. The increase in duration of temperature optimal for asexual reproduction (budding) prolong asexual reproduction and increase the population productivity (Han and Uye, 2010; Willcox et al., 2007). In addition, winter seawater temperature below 6 °C ceases budding and, when below 4 °C, it may even cause disintegration of the polyps (Kroiher et al., 2003). Such low winter temperatures were recorded in the past in the NAD (Raicich et al., 2013). In the period between 1934 and 1963, 10 events of seawater temperature below 6 °C were recorded: in 1935, 1938, 1940, 1942, 1947, 1949, 1953, 1954, 1956, and 1963. These events lasted from 11 (in 1956) and to 57 days (in 1942). After 1963, seawater temperature reached the minima below 6 °C only in 5 years (1981, 1985, 1991, 2005 and 2012) and the duration of the events dwindled to few days per year (Fig. 9a). The absence of extreme minima in winters in the NAD, and the increasing trend in seawater temperature during the period between spring to autumn over the last four decades in both areas, lead to environmental changes that probably extended the yearly environmental window for the growth of the local polyp population(s), that during the following winter through strobilation produce young medusae. In contrast, pelagic medusae reproduce sexually and larvae preferentially settle on artificial substrates (Duarte et al., 2013), or on the natural secondary substrate overgrowing artificial foundation (Makabe et al., 2014; Malej et al., 2012). During 1978 and 1996, the proportion of shoreline covered with ferroconcrete structures increased to 48.9% of the total length of the ISJ shoreline, while in the NAD, the installation of offshore platforms increased exponentially from the 1980s onward, thus, providing new overhanging hard substrate suitable for the expansion of the polyp populations. For example, a newly installed floating pier acted as an amplifier of a locally established bloom of the moon jellyfish in the ISJ, increasing the ephyrae export from the new polyp population of 4.3 fold (Makabe et al., 2014). In addition, these artificial structures may act as stepping stones facilitating the expansion of the population (Duarte et al., 2013), enhance connectivity between subpopulations of jellyfish polyps and help sustain existing shore-based subpopulations (Vodopivec et al., 2017). The carrying capacity of the environment (Hočevar et al., 2018) and the competition for space with sessile organisms (Makabe et al., 2014) may inhibit further increase of the polyp population. Nevertheless, the contribution from polyps attached onto newly installed structures through the recruitment into pelagic medusae population cannot be neglected, especially in areas with increasing marine urbanisation. In contrast, in a marine lake in the National Park of the Mljet Island, the Adriatic Sea, with limited human-

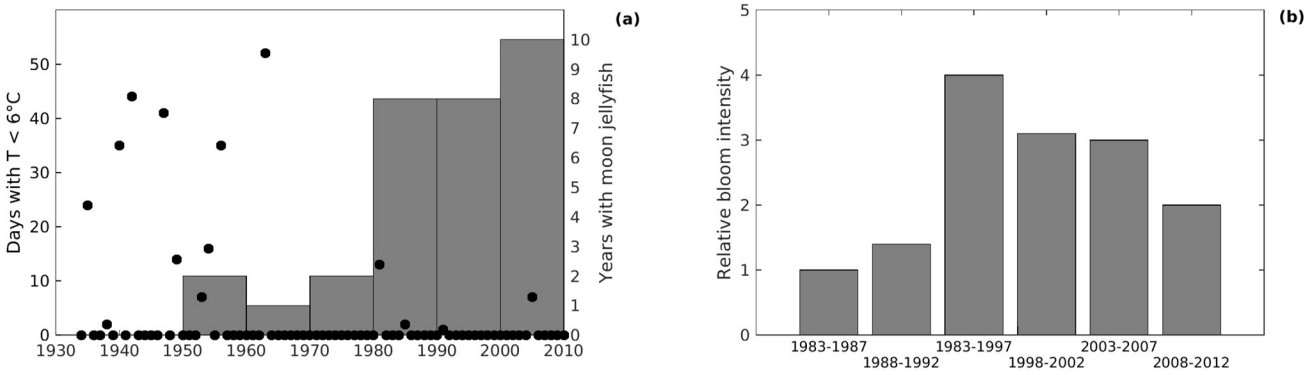

Fig. 9. Observations of moon jellyfish occurrence in (a) the northern Adriatic Sea and (b) the Inland Sea of Japan. Duration of winter periods with extreme low temperatures below 6 °C measured in the northern Adriatic Sea (in (a) marked with filled circles) were more frequent in the years before the late 1960s.

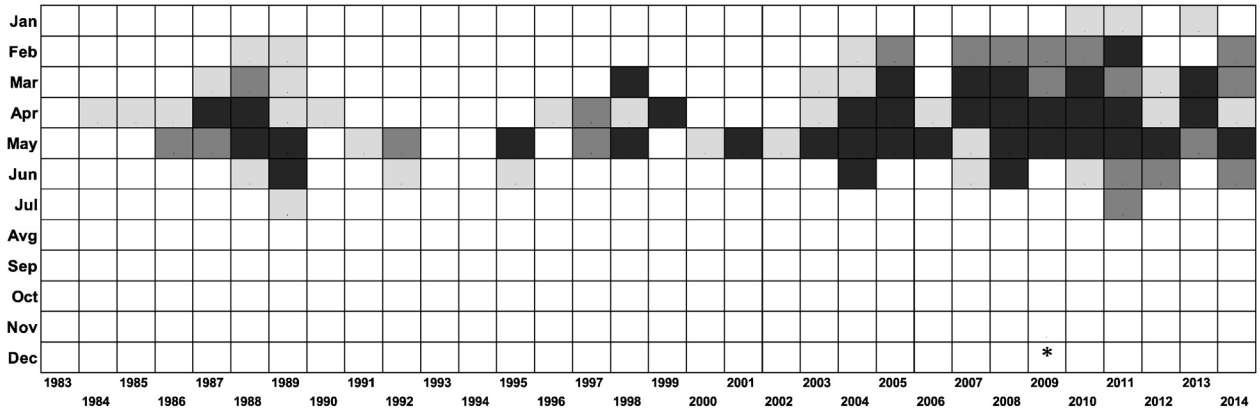

Fig. 10. Inter-annual seasonal occurrence of moon jellyfish in the northern Adriatic Sea between 1983 and 2014 (white - absent, light grey - sporadically present, dark grey - frequently observed few or mass of medusae, and black – blooms; *only one juvenile medusa <2 cm in bell diameter was reported).

induced impacts, the observed changes in plankton community have been associated with larger-scale northern climate processes (Kogovšek et al., 2012; Miloslavić and Lučić, 2015). However, the response of jellyfish to seawater temperature changes in this marine protected area (MPA) were indirect and only affected the medusa stage as polyps were found at depths below the thermocline where the temperature is relatively stable throughout the year (Kogovšek et al., 2012); therefore, in areas with low or absent marine urbanisation, bathymetry may be a more significant factor controlling the stability and seasonality of the moon jellyfish population than temperature.

5. Conclusion

Although we provide only correlative evidence that does not prove causation, we are confident that we have provided sufficient support to hypothesise about human-induced changes (i.e. eutrophication, climate change, overfishing, and marine urbanisation) in promoting moon jellyfish blooms in both study areas. Our results show a synchronous act of large-scale climate drivers (precipitation, river runoff) with man-induced change in nutrient pollution, that resulted in a steady decrease in nutrient discharges into the sea and the increase in the molar

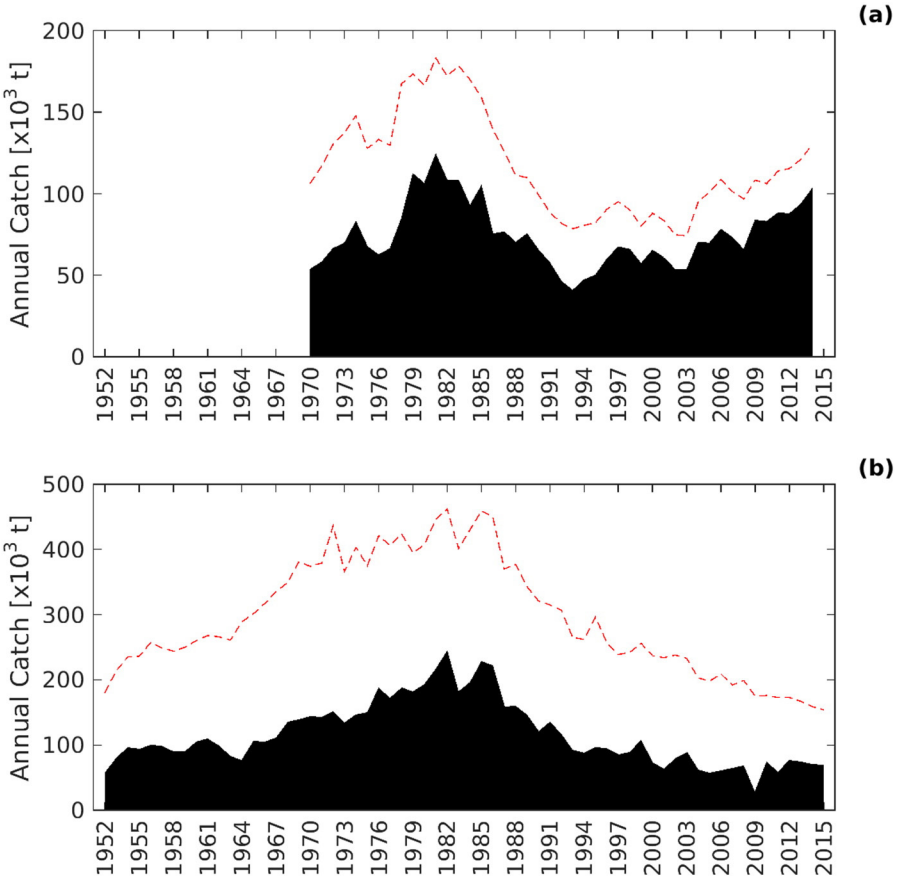

Fig. 11. Annual fish landings in a) the Adriatic Sea and b) the Inland Sea of Japan. Two small pelagic fishes dominated the fish catch: anchovies and sardines (black) with, on average, 46% of total fish catch (red dashed line) in the Adriatic Sea, and 38% in the Inland Sea of Japan.

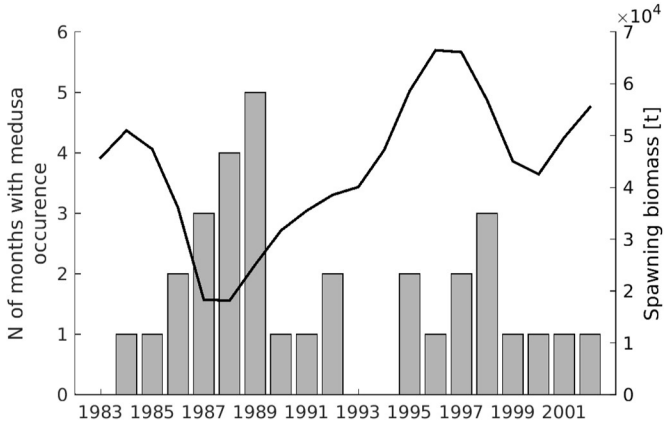

Fig. 12. The number of months in which moon jellyfish were observed during the season of anchovy spawning (March–October) (bars) and the anchovy spawning biomass (black line) (fish biomass data after Cingolani et al., 2003).

N to P ratio. This bottom-up forcing has altered the structure of the marine food web, and in addition to overfishing that relieved the pressure of competition for food with forage fish (the top-down control), the environmental conditions were established that benefited the proliferation of jellyfish. Such numerous medusae then produce even more numerous population of planktonic larvae that eventually settle onto underwater structures. During the extensive marine urbanisation recorded during the last decades, new artificial underwater structures were introduced that provided additional suitable surfaces, and thus promoted the spread of the polyp population. In addition, the increasing trend in seawater temperature has enhanced the asexual reproduction of polyps (budding), maintaining the benthic population at its maximum abundances and, consequently, recruited innumerable propagules into the medusae outburst.

We are currently experiencing a large and increasing cumulative impact of human activities on coastal areas worldwide (Halpern et al., 2015); and, in many of them, we are already recording the outbreaks of jellyfish populations (Purcell, 2012, this study). Currently, there are no effective management plans or actions to mitigate the outburst of jellyfish populations and these results may be used as a foundation for management strategies that could be adopted as a conceptual framework in managing jellyfish population outbreaks. For example, a lower-risk control option may be habitat improvement, or restoration of ecosystem functioning and biodiversity by improving fisheries management (Bax et al., 2001) and systematic conservation planning (Davies et al., 2017; Waldron et al., 2017). On the other hand, higher-risk methods may be implemented for a more rapid and effective control to be applied on one or both life stages. For instance, a local management program to extract medusae with fishing vessels (Ruiz et al., 2012) may reduce the spawning population and consequently, mitigate the recruitment of pelagic larvae into benthic population. In addition, maintenance of underwater artificial structures by implementing antifouling actions may reduce or eliminate the perennial polyp colonies and thus hamper the medusa population outburst (Hwang et al., 2016). At this point we are willing to speculate, that without sustainable management to subsidise the impact of human-induced pressures on the oceans, more coastal areas will be affected by massive and recurrent jellyfish blooms. With the effort to restore such environment, we need to understand how present ecosystems are changing under anthropogenic forcing. In doing so, it is crucial that we disentangle natural fluctuations from changes driven by anthropogenic stressors, before any management operations are taken action. Long-term monitoring networks, such as LTER network, provide coherent environmental data for comprehensive ecosystem research (Haase et al., 2018; Mirtl et al., 2018) and was proven as a valuable asset in identifying ecosystem responses to human-induced pressures (e.g. Jourdan et al., 2018; this study).

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